remained bound at both stages (Figure 1A,B). These results illustrate that DCC distribution is dynamically specified by developmental changes in gene expression.

The aspect of transcriptional activity recognized by the DCC is unknown. Possibilities include chromatin features (e.g., nucleosome-free regions or variants and modifications of histones), or the transcription machinery itself. One suspect is histone H3 K4 methylation, a ubiquitous mark of active promoters. *C. elegans* DPY-30 is homologous to a subunit of the conserved COMPASS complex that establishes H3 K4 methylation, and DPY-30 is required both for normal levels of this modification and for localization of some DCC subunits to the X chromosome (reviewed in [6]).

The most puzzling aspect of transcription-dependent DCC spreading is its purpose. The observation that more DCC tends to bind more highly expressed promoters suggests that it acts locally, repressing individual genes in proportion to their degree of transcription. But contradictory to that model, a genome-wide analysis of gene expression in dosage compensation mutants found little correlation between genes that undergo dosage compensation and those that have DCC bound to their promoters [12]. Moreover, Ercan *et al.* [2] did not detect repression of autosomal genes into which the DCC had spread on X;A fusions. A remaining enigma is why DCC localization is tuned to underlying transcription state and yet, by gene expression profiling, the DCC does not seem to directly regulate transcription of genes at which it localizes. Perhaps spreading generates a sufficient number and distribution of DCC sites to achieve a global reconfiguration of chromosome architecture, analogous to condensin action during mitosis. Alternatively, like mammalian X inactivation or Polycomb repression of *Hox* genes, the DCC could relocate the X into a repressive nuclear compartment [3,7,15]. Condensin facilitates the nuclear clustering and silencing of tRNA loci in *Saccharomyces cerevisiae*, suggesting it could play such a role [16].

In multiple examples of domain-wide gene regulation, evolution has converged on a common strategy of sequence-specific recruitment and sequence-independent spreading [1]. An advantage of this strategy is that specificity need only be conferred to a small number of DNA sequences and recruitment proteins. General spreading can subsequently propagate regulation over an entire domain. The reports covered here have significantly advanced our understanding of one such system. These studies also raise new questions about how the transcription-influenced localization of the *C. elegans* DCC along the X relates to its function in dosage compensation. Elucidating this mechanism is a major challenge for the future.

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Animal Culture: Chimpanzee Table Manners?

Experimentalists interested in chimpanzee culture have focused on captive populations as these could be subject to controlled testing. A new method may allow for sophisticated experimentation under field conditions.

Josep Call and Claudio Tennie

How would an Italian eat Sushi if she had never seen someone use chopsticks before? Presumably she would follow the table manners that she was raised with and would use a fork. Culture shapes human behaviour from infancy and strongly influences our responses as adults in novel situations, often creating both within-group uniformity and between-group variability. Particularly striking are those cases in which between-group differences cannot be simply attributed to ecological (or genetic) differences between groups.

The notion that chimpanzees, just like humans, are also influenced in this way by culture is a hotly debated issue [1]. Yet, something looking like table

Figure 1. Chimpanzee observed while feeding. (Photo: copyright MPI EVA.)

manners has now been found in wild chimpanzee populations [2]. As they report in this issue of *Current Biology*, Gruber *et al.* [2] presented two adjacent chimpanzee populations with the chimpanzee equivalent of our Sushi example: they drilled holes with two different depths into wooden logs and filled them with honey. Honey in shallow holes could be extracted with the fingers, whereas honey in the deep holes required the use of a tool. The two chimpanzee groups differed in their approaches to getting the honey: one group used their hands as well as tools made of leaves, while the other group used sticks (Figure 1).

This finding is important because the preference for sticks or leaves was consistent within each group and it matched the chimpanzees' natural foraging techniques in other situations. In particular, chimpanzees from one site usually use leaves to extract liquids from holes and crevices, while those from the other site usually use sticks. Additionally, by carefully choosing the two chimpanzee groups, the authors were able to make genetic and environmental explanations of the observed differences unlikely. This is the clearest evidence to date that, when presented with an identical problem, chimpanzee groups can differ strikingly in their approach to solve it. Although this finding will fuel the debate on chimpanzee culture, it is unlikely that it will resolve it. Whereas some authors will interpret this finding as evidence of cultural knowledge, others will argue that it falls short of proving it. Why is this so? The answer lies in the differential emphasis that these two warring camps place on two of the key aspects that define culture: group differences and social learning.

Documenting between-group differences (paired with within-group homogeneity) — ideally in the absence of genetic and environmental population differences — has been the approach traditionally used by proponents of the idea that chimpanzees possess culture. Other scholars have instead emphasized the role that social learning plays in human culture. These authors argue that, unless certain forms of social learning are demonstrated, it is not justified to equate human and nonhuman culture, no matter how large the differences between groups are. Because Gruber *et al.* [2] noted that the different solutions of the two chimpanzee populations are not a direct result of social learning — the two populations spontaneously arrived at their preferred solutions or else it was not possible to show that the first method used spread via social means — there is little that the current data can do to convince the sceptics.

As Gruber *et al.* [2] argue, it is very likely that the two different chimpanzee feeding techniques (hand/leaves versus sticks) are the result of previous experience of the two groups, but it is unclear how much and what type of social learning took place during that experience. Given what we know about chimpanzee social learning in the laboratory, a social learning contribution of some sort might be a safe assumption, but it is an assumption that should be tested. Despite the hundreds of papers that have been published on chimpanzee culture, social learning remains largely unexplored in wild chimpanzee (and indeed other primate) populations — something that is quite surprising given that social learning has already been successfully investigated in other taxa in their natural habitats [3–5].

Despite these doubts about how effective Gruber *et al.*'s [2] findings will be in helping establish bridges between the two shores of the chimpanzee culture debate, we are more optimistic about the impact that this study could have on future research, as it paves the way for testing social learning in the wild. Indeed, this type of natural experiment [6], together with laboratory studies on naturally occurring behaviours, can be a powerful combination for investigating social learning. Recent laboratory studies have investigated the origins of certain plant-processing behaviours observed in wild ape populations — such as leaf folding or nettle feeding [7,8]. Quite unexpectedly, these studies found that naïve individuals produced some key aspects of the behaviours without the benefit of social learning, thus forcing us to re-evaluate our assumptions regarding the importance of social learning in the acquisition of certain behaviours. Moreover, those findings serve us as a reminder of how easy it is to underestimate chimpanzees' remarkable individual problem solving abilities.

We have recently argued that many of the behaviours displayed by apes may be reinvented rather than copied from other individuals — given the right conditions [9]. In our view, this is what may have happened in the case reported by Gruber *et al.* [2]: all three types of behaviour exhibited by the tested chimpanzees toward the honey-logs are behaviours that can

be invented by single chimpanzees. Once invented, other chimpanzees become more likely to express the same behaviour themselves — after all, the onlookers could have invented the behaviour themselves, it just happened that another lucky (or perhaps slightly more gifted or motivated) chimpanzee came first and thus acted as a catalyst for the others' individual learning. Furthermore, in the past, group A invented the use of leaves. while group B invented the use of sticks — and both behaviour patterns then stayed via such mechanisms with their groups. As a consequence, group A will be more likely to explore their world with leaves, while group B will be more likely to use sticks (this we have called the 'founder effect'). The time has come to put hypotheses like this to the test.

In conclusion, although Gruber *et al.* [2] have documented the striking different solutions adopted by two chimpanzee groups when solving the same problem, it is unlikely that they will contribute decisively towards the resolution of the chimpanzee culture debate. But the use of this method in the field represents an important advance that could bring social learning under experimental scrutiny in the field and pave the way to investigate the roots of other aspects of human culture such as conformity, normativity and the accumulation of knowledge.

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Mating-System Evolution: Succeeding by Celibacy

Orchids are celebrated for their extraordinary diversity of floral strategies, but species with separate sexes are exceedingly rare. A new study shows that females are maintained with hermaphrodites in one such species through an unusual mix of sexual and asexual reproduction.

John R. Pannell

The great majority of angiosperms are hermaphroditic. Although separate sexes have arisen on numerous independent occasions throughout angiosperm evolution [1], the high frequency of hermaphroditism in most plant families suggests that maintaining both male and female structures within each flower has widespread advantages. One potential benefit of hermaphroditism is the possibility of self-fertilization [2]. Self-fertilization has indeed evolved frequently in plants, in many cases probably in response to selection for reproductive assurance in the absence of mates or pollinators [3–5]. Yet most hermaphrodite plants avoid selfing and possess a range of intricate mechanisms that promote outcrossing [2,6,7]. Such mechanisms are nowhere more striking than the morphological 'contrivances', as Darwin called them, in the orchid family (Orchidaceae) [7].

The Orchidaceae is the largest and one of the more morphologically diverse families of land plants, with around 22,000 species in almost 800 genera [8]. Remarkably, in contrast with its frequent occurrence in other large clades, dioecy (separate males and females) is known only from two orchid genera: *Catasetum* and *Cycnoches* [9,10]. Exceptional cases in biology are often surrounded by exceptional circumstances, and no less so in *Catasetum*. In these orchids, the vehemence with which pollinia, the specialised bags of pollen held on a sticky stalk, are thrust upon unsuspecting pollinators' bodies is so disagreeable to the insects that they subsequently avoid all contact with flowers with the same appearance [10]. This would be counterproductive in populations with monomorphic flowers, because pollinators must of course fly from a pollen donor to a pollen recipient of the same species. But *Catasetum* populations are sexually dimorphic, and the agitated pollinators move away from males, bearing their pollinia, to the flowers of females that have a morphology so different that taxonomists once assigned females and males of *Catasetum* to different genera [10]!

Huang *et al.* [11] have now pieced together a puzzle that would seem to explain a similarly unusual case of the maintenance of gender dimorphism in orchids. Populations of the Chinese orchid species *Satyrium ciliatum* were known to comprise mixtures of normal hermaphrodites with females (a sexual system known as 'gynodioecy'). Gynodioecy is relatively common in flowering plants, but *Satyrium ciliatum* is the only known case of it in the orchids. The proportion of females in *S. ciliatum* is highly variable, ranging from zero all the way to one. High variation in the sex ratio is typical of gynodioecious species [12,13], so what is unusual about gynodioecy in *S. ciliatum*?

The frequencies of females in gynodioecious species are known to depend on a number of factors, including the relative rates of